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DEPLETION OF SOIL MOISTURE BY TWO COLD-DESERT BUNCHGRASSES AND EFFECTS ON PHOTOSYNTHETIC PERFORMANCE

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ABSTRACT—This study compared the abilities of two cool-season bunchgrasses to extract moisture from a drying soil and compared photosynthetic and stomatal responses of the two species as soil moisture supplies were depleted. When grown in 49-L pots in a greenhouse, *Leymus cinereus* extracted more water from the soil and maintained higher gas exchange rates to lower absolute amounts of soil water than did *Agropyron desertorum*. The soil water content at the lower limit of extraction was 10.3% for *L. cinereus* and 13.3% for *A. desertorum*. When soil moisture was expressed as extractable soil water, there was little difference between the species in pattern of water use. Both species maintained high stomatal conductances (g_s) and photosynthetic rates (A) until extractable soil moisture was reduced to about 15%. For field-grown plants under severe water stress, A was higher in *L. cinereus* than in *A. desertorum* at comparable leaf water potentials. The relationship between A and g_s was similar for the two species; the higher A in *L. cinereus* was a consequence of higher g_s . Thus, higher A in *L. cinereus* is achieved through some sacrifice of water-use efficiency.

Key words: extractable soil water, leaf water potential, stomatal conductance, water-use efficiency, *Leymus cinereus*, *Agropyron desertorum*.

Plant species vary widely in their tolerance of seasonal drought and in the mechanisms they use to cope with declining supplies of soil moisture. Some species tolerate seasonal drought by maintaining high leaf water potentials through stomatal closure (Turner 1979). Although they may maintain a high photosynthetic capacity, low stomatal conductance will severely restrict carbon gain under prolonged drought. In contrast, other species allow their leaf water potentials to drop as soil water potentials decline (Turner 1979). This enables the plant to continue to extract water from a drying soil, but decreases in leaf water potential typically are accompanied by decreases in photosynthetic capacity and stomatal conductance (Jones 1973,

Comstock and Ehleringer 1984, Ehleringer and Cook 1984, DeLucia and Heckathorn 1989, Chaves 1991) as well as changes in the diurnal patterns of gas exchange (Schulze and Hall 1982, Tenhunen et al. 1987). It clearly would be advantageous for such species to maintain photosynthetic rates as high as possible as soil and plant water potentials decline.

As plants extract water from a drying soil, the amount of plant-available water decreases exponentially with decreasing water potential (e.g., Slatyer 1967, Fig. 3.3). Consequently, the volume of water gained by a plant in drying a given volume of soil to -2.0 MPa over that gained in drying a soil to -1.5 MPa, for example, is so small that it would seem rather negligible in

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terms of total carbon gain. Jordan and Miller (1980) and Jordan et al. (1983) estimated that the additional water made available to a crop as a consequence of lowering leaf water potential "a few bars" would support transpiration only for 3 or 4 days in the absence of additional root growth. Thus, there would seem to be little advantage in making the necessary osmotic adjustment and/or other leaf modifications to tolerate very low water potentials, and we might expect little difference among drought-tolerant species in their lower limit of extraction of soil moisture. [We use Ritchie's (1981) definition of the lower limit of extraction: the amount of water remaining in the soil when plant growth and activity completely stop.]

On the other hand, tolerance of very low plant water potentials may offer advantages other than gaining more water from a particular volume of soil. Osmotic adjustment may enable a plant to maintain turgor in growing roots which, in turn, would enable the plant to explore the soil for additional water reserves (Sharpe and Davies 1979, Jordan et al. 1983, Westgate and Boyer 1985, Turner 1986). Drought-tolerant sagebrush (*Artemisia tridentata*) plants of the Great Basin of North America move water at night along a hydraulic gradient in the roots from deep in the soil to drier soil at shallow depths (Richards and Caldwell 1987, Caldwell and Richards 1989). The water deposited in those shallow layers can be extracted the following day to support carbon gain or other physiological activity. Finally, Caldwell (1985) postulated that drying a soil to a very low water content may be a way of excluding competitors. These arguments and results suggest that significant but possibly subtle differences could exist in the lower limit of extraction of soil water among species. Indeed, Sinclair and Ludlow (1986) found small differences in the lower limit of extraction among four tropical legumes grown in pots.

Anderson et al. (1987) compared the seasonal patterns of soil water extraction among four drought-tolerant, cold-desert species. They found little difference in the lower limit of extraction among the four species when grown in monocultures on a common soil; however, there was some indication that the native bunchgrass *Leymus cinereus* Scribn. & Merr. A. Löve might be able to extract more water from a soil than could the introduced species *Agropyron desertorum* (Fisch. ex Link) Schult. In addition,

preliminary gas-exchange data from field-grown plants (J. Anderson unpublished data) suggested that *L. cinereus* plants maintained higher photosynthetic activity and had higher stomatal conductance at low leaf water potentials than did *A. desertorum* plants. To test those possibilities, we conducted a greenhouse experiment (1) to compare photosynthetic and stomatal responses of these two species to drying soil and (2) to compare the lower limit of extraction of the two species. In addition, we compared photosynthetic capacity and conductance of the two species under water stress imposed naturally in the field. Both laboratory and field data support the hypothesis that, in comparison to *A. desertorum*, *L. cinereus* plants deplete soil moisture reserves more completely and maintain higher photosynthetic rates as water supplies are diminished; but this is achieved through some sacrifice in water-use efficiency by *L. cinereus*.

METHODS

Plant Materials

Leymus cinereus is a robust tussock grass native to cold deserts and lower mountain slopes throughout the Intermountain West of North America. It occurs on alkaline or saline lowland sites as well as nonsaline upland sites, often on deep soils (Young and Evans 1981, Walker and Brotherson 1982). Plants used in this study were transplanted from a near monocultural natural stand at the Idaho National Engineering Laboratory (INEL). Additional information concerning the ecophysiology of *L. cinereus* can be found in Anderson et al. (1993).

Agropyron desertorum is a tussock grass native to the steppes of Asia; it is naturalized in western North America, where it has been used extensively for rangeland rehabilitation. Stands established by seeding often persist as near monocultures (Marlette and Anderson 1986). Plants used in this study were transplanted from seeded stands at the INEL. Additional information about the ecophysiology of *A. desertorum* can be found in Nowak and Caldwell (1984, 1986) and Nowak et al. (1988).

Greenhouse Studies

Twenty-four pots were constructed from polyvinyl chloride pipes; each pot was 1 m tall and 0.25 m in diameter. The pots were filled with a 1:1:1 mixture of Baccto potting soil, sand, and a clay-loam soil used in experimental field

plots at the INEL (see Field Studies). The mean (and standard error) dry mass of soil placed in the pots was 44.4 ± 0.4 kg. At field capacity that volume of soil held 18.5 ± 0.1 L of water, or 39.7% water by volume. Dormant *A. desertorum* and *L. cinereus* plants were collected from stands at the INEL in November and held at 5°C until 12 plants of each species were transplanted into the 49-L pots in December. The plants were placed in a greenhouse where they received natural sunlight supplemented by four 1500-W metal halide lamps. The height of the lamps was set so that photosynthetic photon flux density (PPFD) at canopy height was 1500–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at midday. The photoperiod was 13 h.

Plants were fertilized twice a week with full strength Ruakura nutrient solution (Smith et al. 1983). After the plants became well established, six of each species were assigned randomly to a well-watered (control) treatment, and the other six were assigned to a water-stress treatment. The well-watered plants received nutrient solution twice a week and distilled water once a week. Water stress was induced by withholding water from the plants for 50 days, after bringing the soil water content to field capacity. Because of the large volume of soil and water in a pot, water stress was imposed gradually, simulating soil drying that occurs naturally under field conditions.

The pots were weighed every 3–4 days during the drying period to determine the amount of water held in the soil of each pot. Soil water content was expressed in two ways. Percent of total soil water (TSW) was defined as (volume of water in the soil) / (volume of water at field capacity) $\times 100$. Extractable soil water (ESW; see Ritchie 1981) was expressed as a percentage of the difference between the volumetric water content at field capacity and that when growth of that species had stopped (day 50 of the drying period). Soil water potential was measured with single-junction, screen-caged psychrometers (J. R. D. Merrill Specialty Equipment, Logan, Utah) placed at soil depths of 150, 350, 550, and 750 mm in three pots per species containing water-stressed plants. Psychrometric output was monitored every 3–4 days using a model NT-3 nanovoltmeter (Decagon Devices Inc., Pullman, Washington).

On day 33 there was a slight increase in the weight of pots in the water-stress treatment (Fig. 1), but it was not until we noted a substantial increase in weight of some pots on day 36 that we realized water had entered some pots

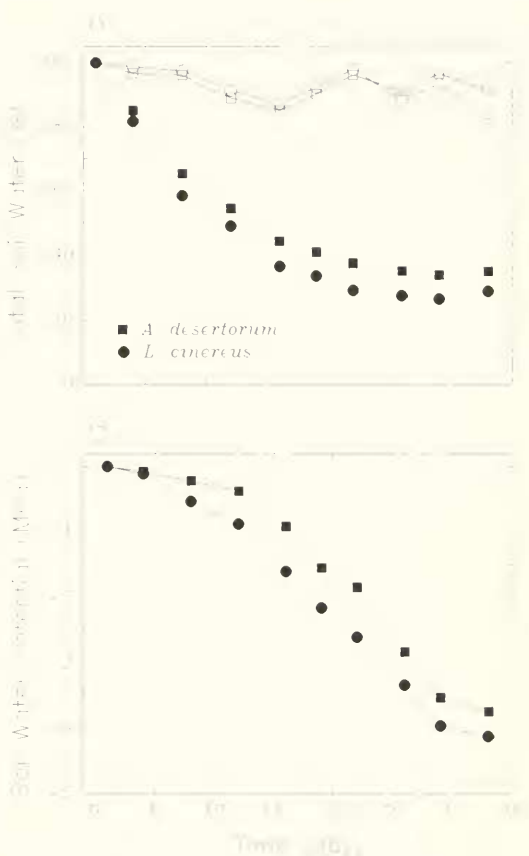


Fig. 1. (A) Changes in total soil water content with time after withholding water from *Agropyron desertorum* and *Leymus cinereus* plants (dashed lines) and for irrigated controls (solid lines) growing in 49-L pots in a greenhouse. (B) Soil water potential vs. time for treatment means corresponding to the closed symbols in A. See Table 1 for statistical analyses.

from pools on the floor resulting from the watering of other plants. After day 36 the amount of water in the soil decreased to levels slightly lower than those on day 29. Because growth of individuals of both species had essentially stopped by day 33 and changes in soil water content after that date were negligible, only data for 33 days are included in most analyses presented here.

Rate of elongation of expanding leaves was used as an index of growth rate. Leaf elongation rate (LER) of the youngest leaf was determined by measuring its length at two times and dividing the difference in length by the time interval. Length measurements were made on two vegetative tillers per pot on three consecutive days each week. Leaf elongation rates reported here were averaged over 45 h.

TABLE 1. General linear models analysis of soil water content expressed as percent of total soil water, soil water content expressed as extractable soil water, elongation rate of the youngest leaf on a tiller, and soil water potential for *Leymus cinereus* and *Agropyron desertorum* plants growing in 49-L pots in a glasshouse. For each dependent variable, main effects were always included in the model, but if interaction terms were not significant, they were excluded from the model. All independent variables in each model were treated as classification variables. There were two levels of species (SP; *A. desertorum* and *L. cinereus*). For all dependent variables in part a, there were two levels of stress (STR; well-watered and water-stressed), and 10 days (DAY) after water was withheld from the the water-stressed plants (1, 4, 8, 12, 16, 19, 22, 26, 29–33). For soil water potential in part b, there were four levels of soil depth (DP; 150, 350, 550, 750 mm) and 9 days (DAY; 4, 8, 12, 16, 19, 22, 26, 29–33).

(a)	Effect:	Species	Stress	Day	SP × STR	SP × DAY	STR × DAY	SP × STR × DAY
Total soil water <i>n</i> = 228		$P < .0001$	$P < .0001$	$P < .0001$	$P < .0002$	–	$P < .0001$	–
Extractable soil water <i>n</i> = 228		n.s. ¹	$P < .0001$	$P < .0001$	–	–	$P < .0001$	–
Leaf elongation rate <i>n</i> = 255		$P < .0001$	$P < .0001$	$P < .0001$	$P < .0001$	$P < .0002$	$P < .0001$	$P < .0003$
(b)	Effect:	Species	Depth	Day	SP × DP	SP × DAY	DP × DAY	SP × DP × DAY
Soil water potential <i>n</i> = 204		$P < .002$	$P < .0001$	$P < .0001$	–	–	–	–

n.s. = not significant

Field Studies

The field studies were conducted at the INEL Experimental Field Station where monocultures of *A. desertorum* and *L. cinereus* were established by transplanting mature individuals from nearby stands to experimental plots having a homogeneous soil to a depth of 2.4 m (see Anderson et al. 1987 for details). The soil consisted of 26% sand, 54% silt, and 20% clay and had a bulk density of 1.28 g cm⁻³. The measurements reported here were made during the third growing season after the plants were transplanted.

Gas Exchange and Plant Water Potential Measurements

Net photosynthesis (A), transpiration (E), and leaf conductance to water vapor (g_w) were measured on the youngest, fully expanded leaves, or on the penultimate leaf on a tiller after inflorescences developed, with an open, compensating gas-exchange system which has been previously described (Nowak et al. 1988, Toft et al. 1989). Gas-exchange measurements of greenhouse-grown plants were made at a leaf temperature of 25°C, a PFD of 1900–2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$, and a leaf-to-air water vapor gradient (v)

of 2 kPa. The concentration of CO₂ inside the cuvette was 330–340 $\mu\text{L L}^{-1}$. Light was provided by a 150-W quartz halogen projector bulb. Measurements were made periodically throughout the drying period between 0900 and 1600 hours; TSW in the pot was determined immediately after gas-exchange measurements.

For gas-exchange measurements in the field, leaf temperature was 24°C, PFD was 1900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ or greater, v was 2.3 kPa, and CO₂ concentration inside the cuvette was $335 \pm 5 \mu\text{L L}^{-1}$. Light was from sunlight or a 150-W projector lamp. Measurements were made in June and early July between 0830 and 1500 hours.

Leaf water potential (ψ) was measured with a pressure chamber (PMS Instruments Co., Corvallis, Oregon) immediately after gas-exchange measurements on the same leaf.

Calculations and Statistical Analyses

A, E, and g_w (leaf plus boundary layer) were calculated according to Caemmerer and Farquhar (1981). Ambient atmospheric pressure at the INEL is about 85 kPa (field measurements) and at Pocatello, Idaho, is about 86 kPa (greenhouse measurements). Statistical analyses were

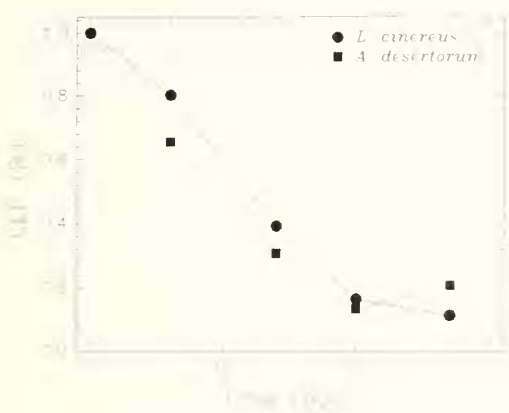


Fig. 2. Relative leaf elongation rate (LER) of the youngest leaf on vegetative tillers, expressed as a percentage of controls, vs. time after withholding water from *Agropyron desertorum* and *Leymus cinereus* plants growing in 49-L pots in a greenhouse. See Table 1 for statistical analyses.

performed with the general linear models procedure of SAS (SAS Institute 1992).

RESULTS

Following the withholding of water, TSW was consistently lower in pots containing *L. cinereus* than in those containing *A. desertorum* (Fig. 1A). The more rapid decline in TSW in *L. cinereus* pots early in the experiment may reflect the larger size of that species, but, if plant size or growth rate was responsible for observed species differences in TSW, differences would have diminished with time. That did not occur. Thus, the significant species differences and species-by-treatment interaction (Table 1a) show that water-stressed *L. cinereus* plants were capable of extracting more water from the soil than were stressed *A. desertorum*. The volumetric soil water content at the lower limit of extraction (day 50) was 13.3% and 10.3% for *A. desertorum* and *L. cinereus*, respectively.

The time courses of soil water potential, averaged over all four positions in a pot and over all pots with water-stressed plants, are shown in Figure 1B. Water potential depended on location within the pot (Table 1b), with lower water potentials occurring at higher positions in the soil profile. Soil water potentials in pots containing *L. cinereus* were significantly lower than those of *A. desertorum* after day 5 (Fig. 1B, Table 1b).

For well-watered plants, elongation rate of the youngest leaf on a tiller (LER) for *L. cin-*



Fig. 3. Net photosynthesis (A), leaf conductance to water vapor (g_s), and intercellular concentration of carbon dioxide (c_i) for *Agropyron desertorum* and *Leymus cinereus* plants vs. total soil water in 49-L pots. The curves were fitted using an inverse secant transformation of soil water content; see Table 2 for equations and values of constants. Measurements were made at a leaf temperature of 25°C, a leaf-to-air vapor pressure gradient of 2.0 kPa, an ambient CO_2 concentration of 330–340 $\mu\text{L L}^{-1}$, and a photosynthetic photon flux density of 1900 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$.

ereus (50.5 mm da^{-1}) was nearly twice that for *A. desertorum* (26.0 mm da^{-1}). Relative LER of both species decreased within 6 days after water was withheld from the stress-treatment plants (Fig. 2). Early in the period of soil drying, relative LER of stressed plants was lower for *A. desertorum* than for *L. cinereus*, resulting in a significant species-by-stress interaction (Table 1). This suggests that leaf elongation may be more sensitive to water stress in *A. desertorum* than in *L. cinereus*.

Table 2. Analysis of covariance of photosynthesis, leaf conductance to water vapor, and intercellular CO_2 concentration for *A. desertorum* and *L. cinereus* plants grown in 49-L pots in a glasshouse (see Fig. 3). The classification variable was species (SP), *A. desertorum* (Agde) and *L. cinereus* (Leci). The covariate (X) was a transformation of total soil water (TSW) expressed as percent of the water content at field capacity. The general form of the transformation is $X = X_0 + \text{sec}^{-1}(\text{TSW} - C)$ where sec^{-1} is the inverse secant function and C is a constant, determined by iteration and given here for both species.

Effect	Species	TSW	SP \times TSW	Constant		R^2	
				Agde	Leci	Agde	Leci
Photosynthesis n = 16	$P < .004$	$P < .0001$	$P < .004$	-26.0	-7.5	.86	.83
Conductance n = 16	$P < .04$	$P < .0001$	—	-26.5	-13.9	.83	.83
Intercellular CO_2 n = 16	$P < .002$	$P < .005$	$P < .004$	-27.1	-19.5	.67	.86

The relationship between A or g_w and TSW for both species is shown in Figure 3. To facilitate statistical analyses, numerous models were fitted to the data by linear regression and transformation of the dependent and/or independent variable. The model that consistently provided the best fit considering all data sets was:

$$Y = b_0 + b_1 \sec^{-1}(\text{TSW} + C)$$

where Y is net photosynthesis or leaf conductance, sec^{-1} is the inverse secant function, C is a constant, b_0 is the intercept, and b_1 is the slope. The constants were determined iteratively by substituting values for them until the highest coefficient of determination (R^2) was obtained. Values of C and R^2 are given in Table 2 for the curves shown in Figure 3.

Analyses of covariance were performed for each gas-exchange variable using species as a classification variable and the inverse secant transformation of TSW as the covariate (Table 2). *L. cinereus* had higher A and g_w than *A. desertorum* at both high and low levels of TSW (Fig. 3, Table 2). When soil water availability was expressed in relative terms, i.e., ESW, the responses of the two species were similar. Both maintained high A and g_w until extractable water content reached about 15%; marked reductions of A and g_w occurred at lower levels of ESW (data not shown).

Intercellular CO_2 concentrations (c_i) were higher in leaves of *L. cinereus* than in *A. desertorum* over a wide range of soil water contents (Fig. 3, Table 2). Therefore, under comparable atmospheric conditions *L. cinereus* lost more

water per unit of carbon gained than did *A. desertorum*, which reflects the additional cost of water paid to achieve higher A.

A and g_w of plants sampled in the field in late spring and early summer were positively correlated with ψ measured concurrently (Fig. 4). For both species, A was more closely correlated with ψ than was g_w , and the correlation coefficients were higher for *L. cinereus* than for *A. desertorum*. At the time field sampling was initiated, *L. cinereus* plants were considerably more water stressed than were *A. desertorum* plants because of differences in ESW in the plots at the beginning of the growing season (data not shown). This difference is reflected by the highest ψ values recorded for the two species (Fig. 4). As a consequence, the highest rates of A were lower for *L. cinereus* than for *A. desertorum* and were considerably lower than the maximum A of *L. cinereus* observed in the greenhouse (Fig. 3) or for well-watered plants in the field (Anderson et al. 1993). That most *L. cinereus* plants were stressed while some *A. desertorum* were not may account for the higher correlation coefficients for *L. cinereus*. Data in Figure 4 indicate that A and g_w were generally lower in severely stressed *A. desertorum* than in *L. cinereus* at comparable ψ , which is consistent with findings from the greenhouse study.

The relationship between A and g_w is similar for the two species when grown either in the field or greenhouse (Fig. 5). This again demonstrates that the higher A in *L. cinereus* was a consequence of higher g_w rather than a higher photosynthetic capacity. Field-grown plants had



Fig. 4. Net photosynthesis (A) and leaf conductance to water vapor (g_w) for field-grown *Agropyron desertorum* and *Leymus cinereus* plants as a function of leaf water potential, measured concurrently. Gas-exchange measurements were made at leaf temperature of 24°C, a leaf-to-air vapor pressure gradient of 2.3 kPa, an ambient CO_2 concentration of 330–340 $\mu L L^{-1}$, and a photosynthetic photon flux density 1900 $\mu mol photons m^{-2} s^{-1}$. Trend lines were fitted by linear regression with leaf water potential taken as the independent variable (solid line = *L. cinereus*, dotted line = *A. desertorum*).

higher A for a given g_w compared to greenhouse-grown plants (Fig. 5). The intercept of the regression of g_w on A did not differ significantly from zero for field-grown plants, indicating that WUE was quite constant over the range of A and g_w measured (Schulze and Hall 1982). However, the regression line did not pass through the origin for plants grown in the greenhouse ($P < .05$), which suggests that WUE decreased with increasing A and g_w .

DISCUSSION

Results of the greenhouse study confirmed our suspicions, based on data from monocultures grown in the field (see Anderson et al.



Fig. 5. Leaf conductance to water vapor (g_w) versus net photosynthetic rate (A) for *Agropyron desertorum* and *Leymus cinereus* plants grown in the field (closed symbols) or in a glasshouse (open symbols). Gas-exchange measurements were made over a wide range of soil water availabilities; cuvette conditions were the same as in Figure 4. Trend lines for glasshouse-grown plants (solid line) and field-grown plants (dotted line) were fitted by linear regression with A taken as the independent variable (Schulze and Hall 1982).

1987), that *L. cinereus* plants could extract more water from a soil profile than could *A. desertorum*. In addition, *L. cinereus* maintained higher A at low Ψ compared to *A. desertorum*. These data suggest that *L. cinereus* might have a competitive advantage, should the two species co-occur. It is important to remember, however, that *A. desertorum* is naturalized in western North America, and so the species did not co-evolve.

L. cinereus achieved higher A by maintaining a higher g_w through higher stomatal conductances. Thus, there was an additional water cost per unit carbon gained. The large stature of *L. cinereus* plants suggests a high water requirement, and indeed stands of this species can use copious amounts of water (Anderson et al. 1987). As a consequence, *L. cinereus* typically is found on deep soils or areas that receive runoff water from adjacent sites (Miller et al. 1982, Walker and Brotherson 1982, Roundy 1985). On such sites its capacity to dry a soil to lower water contents may exclude potential competitors. Indeed, it often occurs in pure or nearly pure stands on such sites. Sirotiak (1990) showed that there was intense intraspecific competition in a stand of *L. cinereus*, and the *L. cinereus* plants reduced leaf water potentials of

in high-soiling *Chrysothamnus nauseosus* shrubs. The size and lower water-use efficiency of *L. cinereus* are likely disadvantageous, however, on sites where total water available over the growing season is more limited. Mortality of *L. cinereus* plants was greater than that of *A. desertorum* on our experimental field plots during a severe drought in 1957–58 (unpublished observations).

In contrast to *L. cinereus*, *A. desertorum* establishes well and thrives on shallow soils and very arid sites (Rogler and Lorenz 1983). Its success on such sites probably reflects a smaller size at maturity (even under well-watered conditions), the ability to withstand prolonged drought, and prolific production of viable seeds (Hull and Klomp 1967, Marlette and Anderson 1986, Pyke 1990). Caldwell and his colleagues at Utah State University have shown that *A. desertorum* is a vigorous competitor for water and soil nutrients (reviewed by Dobrowolski et al. 1990). Its competitive ability reflects, at least in part, the production of thin roots that enable it to extract water rapidly from the soil (Eissenstat and Caldwell 1988).

It seems probable that the ability of *L. cinereus* to reduce soil water content to lower levels than those of soil supporting *A. desertorum* reflects lower osmotic potentials in leaves of *L. cinereus*. We attempted to estimate osmotic potential of greenhouse-grown plants from pressure-volume curves, but leaves of *L. cinereus* were so brittle that we were unable to obtain reliable data. Concurrent measurements of leaf relative water content (RWC) and water potential of field-grown plants showed that, for a given RWC, *L. cinereus* had lower ψ than did *A. desertorum* (data not shown; $P < .04$ by analysis of covariance). This difference between species could arise from a greater degree of osmotic adjustment (lower osmotic potential at a given RWC) by *L. cinereus* compared to *A. desertorum*.

Kuang et al. (1990) postulate that the factor that causes a reduction in LER as the soil dries also induces osmotic adjustment in the leaves. Their results show that the proportional change in LER per unit osmotic adjustment was much greater in lupin than in wheat, which suggests that LER in a species with greater osmotic adjustment might be less sensitive to the stress imposed by drying soil. Thus, the observation that LER was reduced relatively less in *L. cinereus* than in *A. desertorum* over the

first 3 weeks of the drying period (Fig. 2) also may reflect greater osmotic adjustment in *L. cinereus*.

Previous studies have shown that leaf expansion frequently is more sensitive to water stress than is photosynthesis (Begg and Turner 1976). As reported here for two perennial tussock grasses, Kuang et al. (1990) found that LER in wheat and lupin was reduced almost immediately after withholding water. They demonstrated that LER decreased in response to drying soil even when leaf turgor was maintained, and they suggested that leaf growth, stomatal conductance, and osmotic adjustment are all controlled by the balance of leaf phytohormones as influenced by hormones produced in the roots. Given the frequent observation that A and g_w are closely correlated (e.g., Fig. 5), it would seem reasonable to add photosynthetic capacity to the list.

The relationship between g_w or A and TSW (Fig. 3) indicates a close coupling between leaf gas exchange and soil water content, as has been reported for a number of herbaceous and woody species growing in a variety of soils (Gollan et al. 1985, Turner et al. 1985, Sinclair and Ludlow 1986, Henson et al. 1989). Turner et al. (1985) and Gollan et al. (1985) demonstrated that although g_w and ψ often were correlated, the nature of the relationship was dependent upon environmental conditions and the rate of soil drying. Thus, they found no unique relationship between g_w and ψ and postulated that g_w and A are controlled by the level of water in the soil rather than in the leaf. Subsequent studies have confirmed that hypothesis, showing that the roots "sense" water availability or some related parameter in the soil and transmit signals to the leaves that control their behavior (Gollan et al. 1986, Masle and Passioura 1987, Passioura 1988, Henson et al. 1989, Zhang and Davies 1989, 1991, Tardieu et al. 1991). Our data are consistent with this model; for both species, g_w and A were closely related to soil water content (Fig. 3). Rather than showing a cause-and-effect relationship, the correlations between g_w and ψ (Fig. 4) likely reflect co-variation in response to declining soil moisture supplies.

In conclusion, this study shows that there may be small but significant differences in the extent to which cold-desert species can dry a soil profile. Such differences may be important in competitive interactions (Caldwell 1985). Compared with *A. desertorum*, *L. cinereus* maintains

higher photosynthetic rates as soil moisture supplies decline, but it does so by maintaining a higher conductance, not through a greater photosynthetic capacity.

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